ON THE OCCURRENCES OF *OPISTHIUS RICHARDSONI* KIRBY AND *ASAPHIDION YUKONENSE* WICKHAM (COLEOPTERA, CARABIDAE) AS LATE PLEISTOCENE FOSSILS

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Abstract. – Numerous fossils of the carabids Opisthius richardsoni Kirby and Asaphidion yukonense Wickham are known from late Pleistocene and early Holocene deposits in midcontinental North America. Both species are presently restricted to riparian habitats of the Cordilleran foothills. Their fossil occurrences in the midcontinent are explained by reference to meltwater habitats associated with the growth and decay of the Laurentide ice sheet.

Key Words: Coleoptera, Carabidae, Opisthius, Asaphidion, Pleistocene, fossils

Don Whitehead was always fascinated with a good biogeographic mystery, and this one had him hooked. On a January morning in 1977 at the Smithsonian Institution, Don Whitehead confirmed the identification of a fossil elytron of the western-montane carabid species Opisthius richardsoni Kirby. The specimen was from a 12,500 yr B.P. (years Before Present) fossil assemblage at Norwood, Minnesota (Ashworth et al. 1981). Opisthius richardsoni joined a small, but growing, group of carabid species of western affinities occurring as fossils in midcontinental and eastern sites of late Pleistocene age. The first of these to have been discovered, Asaphidion yukonense Wickham, was from a 10,600 yr B.P. peat deposit in southern Ontario (Ashworth 1977). The question of why species with existing western montane distributions were present in lowland fossil assemblages more than a thousand kilometres to the east of the Rockies was as intriguing to Don as it was to us. On subsequent visits to the Smithsonian, Don would quiz us about the latest ideas that we had to explain the distributions of these species. Those ideas are expressed in

this paper as a tribute to the stimulating conversations that we had with Don.

MODERN AND FOSSIL OCCURRENCES

Lindroth (1961) described the habitat of O. richardsoni as "confined to the banks of rivers and big brooks, on places where the soil is soft, consisting of clay, often mixed with sand and gravel." We have regularly collected this species on sand and gravel bars adjacent to cold, rapidly-flowing waters of streams in the Cordilleran foothills. Populations of this species occur from southern Alaska to Southern California, in a range that Lindroth (1961) described as "pronouncedly western" (Fig. 1).

Fossils of *O. richardsoni* have been recorded from sediments of late Wisconsinan age in northeastern Illinois (Garry et al. 1990b), north-central Iowa (Schwert, ms. submitted), south-central Minnesota (Ashworth et al. 1981), and northwestern Ontario (Schwert and Bajc, unpubl. data) (Fig. 1).

Lindroth (1963) reported that A. yukonense "occurs on the banks of running waters ... often under leaves of Salix and



Fig. 1. The modern and fossil distribution of *O. richardsoni* and *A. yukonense*. The margins of the Laurentide ice sheet are shown at 18,000, 14,000, 11,000, and 8000 yr B.P. (after Dyke and Prest 1987).

Alnus where the vegetation is restricted to patches of tiny mosses." J. V. Matthews, Jr. (pers. comm. 1990) has collected the species on bare patches of loessic soils close to running water. The range of this species is more restricted than that of *O. richardsoni*, occurring in Alaska, Yukon Territory, British Columbia, and west-central Alberta (Fig. 1). Asaphidion yukonense occurs as fossils in deposits of late Wisconsinan age in westcentral Illinois (Schwert and Hajik unpubl. data), northeastern Wisconsin (Morgan and Morgan 1979, Garry et al. 1990a), Vermont (Matthews unpubl. data), southern Ontario (Ashworth 1977, Morgan et al. 1983), and northwestern Ontario (Bajc et al. 1986, Schwert and Bajc unpubl. data) (Fig. 1).

DISCUSSION

The correlation between fossil occurrences and ice margin positions of similar age indicates that *O. richardsoni* and *A. yukonense* were inhabitants of the ice-marginal zone (Fig. 1). The occurrences of *O. richardsoni* at 21,500 yr B.P. at Wedron, Illinois, and at 15,300 yr B.P. at Fort Dodge, Iowa, were associated with the ice advancing to its late Wisconsinan maximum. The remaining occurrences of both species were associated with the ice-margin in the process of retreat, as is reflected by the sequential decrease in ages of fossil occurrences northward (Fig. 1).

Both O. richardsoni and A. yukonense presently occur on sparsely-vegetated banks of rapidly-flowing, meltwater-fed rivers. Riparian habitats of this type are no longer represented in central and eastern North America but were widespread throughout that region during the last glaciation. The vegetation based on pollen analyses of O. richardsoni-bearing sediments at Wedron, Illinois (Garry et al. 1990a), Fort Dodge, Iowa (R. G. Baker pers. comm.), and Norwood, Minnesota (Ashworth et al. 1981), was a mosaic of open areas and patches of spruce woodland.

Opisthius richardsoni and *A. yukonense* were members of insect communities that do not exist today. Non-analogous animal and plant communities characterized the unstable transitional environments of the late Wisconsinan. Community composition continually changed as species with different ecological requirements and dispersal capabilities responded to rapid environmental changes.

What were the conditions that led to the range expansion of *O. richardsoni* and *A. yukonense* into central and eastern regions of North America? We speculate that prior to the last ice advance these species may have had distributions in the Cordilleran foothills similar to those of today. As Laurentide ice advanced southward, meltwaters formed a complex of braided rivers and outwash plains south of the ice margin to the east of the Cordillera. From montane streams, southeastward dispersal of individuals across interfluves produced an eastward range extension for both species. Fossils of O. richardsoni have not been discovered east of Iowa and Minnesota, which during the late Wisconsinan may have been its easternmost range limit. Asaphidion yukonense was evidently more successful in eastward dispersal, as fossils are known from as far east as Vermont. As ice retreated northward, the meltwater stream habitats that had supported O. richardsoni and A. vukonense disappeared from the midcontinent. The loss of habitat resulted in their present range restriction to the Cordilleran foothills.

Opisthius richardsoni and A. yukonense are examples of species that underwent largescale changes in range in response to climate change and glaciation. Occasionally, the combination of climatic change and ice barriers resulted in even more profound biogeographic effects. Fossil assemblages from 21,500 to 14,000 yr B.P. ice-marginal locations in Iowa and Illinois contain arctic species with distributions today restricted to Alaska, Yukon, and the Northwest Territories. We have proposed (Schwert and Ashworth 1988) that the southern populations of these species were extirpated as a result of climatic warming and competition for the ice-marginal environment by warmer-adapted species dispersing into the region from the south. The result of the elimination of populations of arctic species in the midcontinental region was that the Alaska-Yukon refugium became the principal source region for the repopulation of the arctic during the Holocene.

The fossil occurrences of *O. richardsoni* and *A. yukonense* can be understood in terms of the geologic record of environments known to have existed during the late Wisconsinan. The occurrences of other "western" species within these fossil assemblages are less easily explained. For example, the coccinellid *Hippodamia caseyi* Johnson, which today has a range extending from southern British Columbia to northern California and Colorado (Gordon 1985), was present at Fort Dodge, Iowa, 15,300 yr B.P. This species is not riparian, and its distribution cannot be directly linked to the disappearance of a glacially-associated habitat.

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Editor's Note

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